

ECOLOGY OF *CELTIS RETICULATA* IN IDAHO

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ABSTRACT.—The small deciduous tree *Celtis reticulata* (netleaf hackberry) reaches its northern limit in Idaho, where, contrary to most of its western range, it often occurs as an overstory dominant. Two hundred fifty stands of this tree were sampled throughout Idaho. *Celtis* is slow-growing, averaging 4 m tall at 50 yr, and long-lived (to 300–400 yr). It occurs in a variety of habitats, from riparian to rocky uplands. Trees grow best where topographically sheltered, such as in draws and narrow canyons, and where soils are loamy. Although plants grow more slowly as surface rock cover increases, stands are often associated with rock, with a mean surface cover of 39% rock. Differences in growth rates were unrelated to parent material and aspect. Most stands are reproducing, in spite of habitat degradation caused by overgrazing, alien plant invasion, and increasing fire frequencies. Stands are typically represented by one dominant cohort; however, young, even-aged stands are rare and are generally found along waterways on stream terraces or at the high-water line. Although slow-growing, *C. reticulata* shows promise for land managers interested in site enhancement. This native species is long-lived, produces fruit used by wildlife, and provides structural diversity in a semiarid landscape (with a maximum height of 12 m) in areas that are becoming increasingly dominated by exotic plant species.

Key words: *Celtis reticulata*, netleaf hackberry, ecology, Idaho, growth, longevity, stand structure, recruitment, site characteristics, livestock grazing, rehabilitation.

Celtis reticulata Torr. (netleaf hackberry, western hackberry) is a deciduous shrub to small tree in the elm family (Ulmaceae), widely distributed in semiarid regions of the western United States (Fig. 1). It occurs in a diversity of habitats, including deciduous riparian woodlands, mountain shrub, wash scrub, and live oak–mixed shrub communities, in rocky canyons, and as scattered individuals in semi-desert grasslands, pinyon-juniper and Joshua tree woodlands (Glinski 1977, Plummer 1977, Brown 1982, Albee et al. 1988). Its elevational range is from 200 to 2000 m (Elias 1980). Populations are often small or highly localized (Daubenmire 1970, Dooley and Collins 1984), particularly at the northerly latitudes in the states of Oregon, Washington, and Idaho (Eliot 1938). Despite its broad distribution, little is known about the plant's ecology, presumably due to its position as a minor component in many of its habitats, and its fragmented occurrence (Peattie 1953, Lanner 1983).

While *C. reticulata* is sparsely distributed in Idaho, near its northern limit (Fig. 2), it appears to exhibit wide ecological tolerances. However, it tends toward the warmest portions of canyons, especially southerly aspects (Tisdale 1986). It is a member of both riparian and upland communities in Idaho, where it can

occur as a locally abundant, overstory dominant (Huschle 1975, Johnson and Simon 1987). Along the Wiley Reach of the middle Snake River, it forms narrow, but extensive, gallery forests of nearly monospecific stands (Bowler 1981). On steep shoreline escarpments of the lower reaches of the Snake River, in the "Douglas" hackberry vegetation type described by Huschle (1975), it forms a dense, nearly closed canopy. On the gentle shoreline slopes, alluvial fans, and colluvial cones of the lower Snake River, it grows in an open savanna (Daubenmire 1970, Huschle 1975). "Open savanna" is perhaps the best way to describe the appearance of a typical *Celtis* community on an upland site in Idaho, where individuals occur in a random or clumped pattern with extensive areas of grassland between.

Plants produce a small, fleshy drupe in the fall, favored by a variety of birds and mammals (Hayward 1948, Lanner 1983, C. A. Johnson 1990, personal communication). With as many as 41 species of birds associated with *Celtis* communities in Idaho, the tree's importance for wildlife cannot be overemphasized (Asherin and Claar 1976). It provides cover for a variety of big game species, including mule deer and bighorn sheep (Asherin and Claar 1976), as well as much-sought-after shade for domestic

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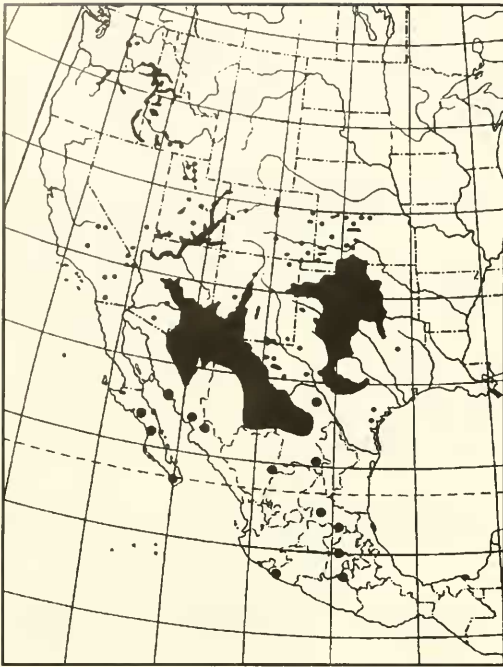


Fig. 1. Global distribution of *Celtis reticulata* (revised from Little 1976).

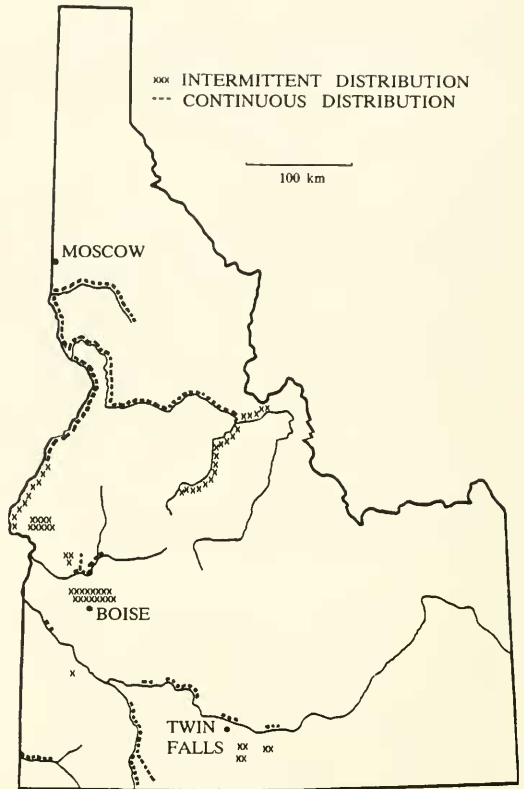


Fig. 2. Idaho distribution of *Celtis reticulata*.

livestock along the Snake River (Daubenmire 1970).

Due to an apparent tolerance of harsh, water-stressed growing conditions, a strong potential to resprout following disturbances such as fire and herbivory, and its high wildlife values, public land managers are interested in using *C. reticulata* to rehabilitate disturbed habitats. However, we must know more of the growth rate, longevity, stand structure, and ecological tolerances of the species to properly evaluate its potential in site enhancement or rehabilitation projects.

This study sought to answer the following questions: (1) What are the growth rates and longevities of *C. reticulata*, and do they differ with aspect, parent material, soil texture, percent surface rock cover, topographic position, topographic shelter, and grazing intensity of a stand? (2) How does the size class structure of *C. reticulata* stands differ with the environmental parameters listed above? Is the species reproducing in Idaho, and does recruitment differ under different environmental conditions? (3) Are environmental conditions related to differences in growth form of the plant (i.e., the formation of single vs. multiple stems)?

METHODS

Field Methods

Two hundred thirty stands spread over much of the Idaho range of *C. reticulata* were sampled in 1990 and 1991. Approximately 20 stands on the west side of the Snake River, in adjacent Oregon and Washington, were also sampled (total $N = 250$). Stands were selected based on within-site homogeneity of apparent history, topography, and parent material, and a minimum population size of six individuals (many more individuals were usually present). With these constraints for homogeneity, the sampling areas were typically irregularly shaped and small, usually less than 0.25 ha. Stands were chosen to represent a range of sites and disturbance histories.

Stands were assigned to topographic positions (Table 1) that included river terrace, high-water line, draw, rocky draw, bench, toe slope, lower slope, broken lower slope, mid-slope, upper slope, and talus. The 11 categories were narrowly defined on the assumption that

TABLE 1. Definitions of topographic positions in which *Celtis reticulata* was sampled.

River terrace	Relatively flat horizontal surface cut or built by river or stream action
High-water line	Transition line between flood-tolerant and -intolerant plant species
Draw	Shallow incision in a slope, with <30% total surface rock cover
Rocky draw	Shallow incision in a slope, with >30% total surface rock cover
Bench	Nearly level surface usually well above active floodplains and terraces
Toe slope	Gently inclined, basal part of a slope continuum that grades to the valley, usually <14° slope
Lower slope	Lower 1/3 of a hillside (above the toe slope, when present); if steep (>14°) and toe slope absent, the basal part of the slope that meets the valley floor
Broken lower slope	Similar to lower slope but with extensive surface cover of large boulders and outcrops
Mid-slope	Middle 1/3 of a hillside, relative to the surrounding landscape
Upper slope	Upper 1/3 of a hillside, relative to the surrounding landscape
Talus slope	Coarse, angular rock fragments derived from and lying at the base of cliffs or rock slopes; slopes typically >25°

combining them at a later time, if needed, would be possible. Based on field observation and reconnaissance, the number of stands sampled within each topographic position was approximately proportionate to how frequently those topographic positions were occupied by the species. Stand-level data recorded, in addition to topographic position, included elevation; latitude; longitude; aspect; slope; percent surface rock cover; surface soil texture; parent material; topographic shelter; grazing intensity; total stand density; density within four structural classes, including seedling, juvenile, mature, and decadent individuals; number of cohort modes; and associated dominant plant species (explained below).

Surface soil textures were evaluated by moistening in the field according to the Soil Conservation Service "Guide for Textural Classification" (Brady 1974). When soils were unreachable due to surface rock, the surface rock matrix was classified instead. For example, stands on talus slopes had soils categorized as "talus."

Six categories of parent material were identified initially, including granite, sandstone, basalt, river alluvium, rhyolite, and oolitic limestone. However, because of the small sample

size of rhyolite (4) and its chemical similarity to granite, the two were combined for analysis. A similar situation existed for oolitic limestone, an uncommon and geographically restricted coarse-grained rock that typically occurred as a lens within sandstone-dominated strata. Therefore, the eight stands on oolitic limestone were combined with sandstone for analysis.

Each stand was categorized by "topographic shelter": open (0), intermediate (1), and sheltered (2). For example, exposed stands growing within a valley were classified as "intermediate," while stands growing in a side canyon of the same valley were classified as "sheltered." "Open" stands were those with unobstructed exposure to solar radiation. They were typically not associated with a major, incised drainage; rather, they faced broad, expansive valleys.

To evaluate recruitment and growth of *C. reticulata* under different livestock grazing pressures, we scored grazing intensity within a stand as none to moderate (1) or extreme (2). Stands scored as extreme were recognized by (1) heavy browsing of trees, with a hedged or "pasture-tree" growth form; (2) elimination of vegetation under trees by trampling; (3) tree roots exposed by soil compaction and erosion; and (4) dominance of alien plant species. Thirty-six of the 250 stands were classified as extreme.

The overall density of *Celtis* stands was categorized as (1) widely scattered [mature individuals more than 10 crown widths apart]; (2) scattered [mature individuals separated by gaps of 4–10 individual crown widths]; (3) sub-continuous [breaks in the total canopy exist but mature individuals average no more than 3 crown widths apart]; or (4) continuous [little open space in the canopy; crowns form a continuous matrix with occasional gaps]. Intermediate sites were recognized with a midpoint value (e.g., 3.5 for stands approaching a closed canopy).

To evaluate the composition of *C. reticulata* stands, densities in four structural classes were also estimated in a similar fashion. The four structural classes were defined as follows: (1) seedling [individual of the year and ≤ 2 yr old]; (2) juvenile [individual >2 yr old and ≤ 1.5 m tall]; (3) mature [>1.5 m tall]; and (4) decadent [>1.5 m tall and experiencing significant dieback, i.e., at least one major dead branch present].

Within each stand at least three individuals, chosen to represent the modal size in the stand, were measured and aged. Modal size was defined as typical size of individuals in the dominant (most abundant) cohort. Measurements recorded for each tree included height, age, diameter at core height (typically 20 cm above ground level), number of live and dead stems, and percent rock cover below the canopy as centered over the main trunk. When two or three modal sizes were present, all modes were sampled for a minimum total of either six or nine individuals. When stands were all-aged with no apparent modal tree size, at least six individuals of the dominant canopy cohort were sampled. The number of modes present, from 1 to 4, with 4 equivalent to an all-aged stand, was recorded as a stand-level variable. Most height measurements were obtained with an 8-m, extendable level rod. For taller trees, height was determined with a clinometer.

Increment cores were taken at the same height the diameter was measured (20 cm). Cores were transported in plastic straws, glued onto slotted boards, sanded, and annual growth rings were counted under a dissecting microscope. When cores did not reach the tree's center (i.e., because of rot), the number of missing years was extrapolated by first subtracting the length of the core from the tree's radius. This remainder was multiplied by the number of rings counted in the core's inner centimeter, which was then added to the number of rings counted for an estimate of the total age. When cores were off-center, the missing radius was estimated by overlaying a clear transparency with a series of circles of known radii over the core, matching the ring pattern in the core with a circle, and multiplying its radius by the number of rings in the centimeter nearest the core's center. This amount was added to the number of counted years to estimate tree age. Small-diameter noncoreable individuals were cut down and a cross section was removed, sanded, and the rings counted as above.

Analytical Methods

Stands were not included in the analysis if the sample size within a particular topographic position or parent material was too small, or if the majority of cores from a stand were illegible after sanding due to contortions in the

radial growth. Nine stands were dropped, for a final sample size of 241. SPSS (1988) was used for all analyses.

A heat load index was generated to account for differences in heat load from northeast- to southwest-facing slopes (Whittaker 1960, Muir and Lotan 1985). For each stand, index values were calculated with the following equation, where Θ = aspect in radians east of north: heat load = $(1 - \cos(\Theta - \pi/4))/2$. Index values ranged from 0 (NE slopes) to 1 (SW slopes).

To compare *C. reticulata* growth rate and stand structure differences under various environmental conditions, we developed 50-yr site indices as measures of growth potential (i.e., site quality), as outlined in Husch et al. (1972). Site index is based on average heights of dominant trees at a specified index age (usually 50 or 100 yr) and is the most widely used method of evaluating site quality for tree growth (Husch et al. 1972, Daubenmire 1976). Site index curves are constructed to allow for estimation of site index for stands older or younger than the index age, as index age stands are seldom encountered (Husch et al. 1972).

The commonly used relationship of tree height to age formed the basis for one index, and the relationship of tree diameter to age formed the basis for the second (DeBolt 1992). The best linear fit was achieved when log (height, m) and log (diameter, cm) were regressed on the log of tree age ($R^2 = .25$, $R^2 = .54$, respectively; $N = 939$). The resulting equations were $\log(\text{height}) = 0.428 \times \log(\text{age}) - 0.135$ and $\log(\text{diameter}) = 0.764 \times \log(\text{age}) - 0.165$. Using these two equations, we obtained the expected (mean) height and diameter at 50 yr, then back-transformed to improve interpretability, yielding an expected size at 50 yr of 3.9 m tall and 13.6 cm in diameter.

For each tree in the data set, the site index was calculated by first finding its residual from the regression line, then shifting this residual to the 50-yr point on the line, which yields an estimated height and diameter at 50 yr. Thus, the equations to calculate site index (SI) for each tree were:

$$\text{Log (height SI)} = 0.591 + (\text{LOGheight} - ((0.428 \times \text{LOGage}) - 0.135))$$

$$\text{Log (diameter SI)} = 1.134 + (\text{LOGdiam} - ((0.764 \times \text{LOGage}) - 0.165))$$

To analyze structural class differences under differing environmental conditions, the variable TYPE, representing types of stand structure, was created. Based on the density of juvenile, mature, and decadent size classes in a stand, the five TYPEs were defined as follows: (1) young (juvenile); (2) mature, nonreproducing, nondecadent; (3) mature, reproducing, nondecadent; (4) mature, reproducing, decadent; and (5) mature, nonreproducing, decadent (Table 2).

Based on field observations, mortality of *C. reticulata* seedlings during year one is extremely high. Because most seedlings were yearlings, seedlings were not used to define TYPE. Stands were classified as reproducing when the juvenile density class was 1 or greater (i.e., ≥ 5 individuals).

Celtis reticulata growth rate, expressed by site indices, was analyzed as the dependent variable in one-way analyses of variance (ANOVA) against the environmental parameters topographic position, parent material, soil texture, grazing intensity, and topographic shelter. Relationships between site indices and ordered categorical independent variables were analyzed by linear regression. With few exceptions, height site index was a more sensitive predictor of growth differences than diameter site index. *Celtis reticulata* growth rates and relationships with topographic position and other environmental parameters were also analyzed with analysis of covariance, to combine categorical and continuous factors. Included in the model was the categorical variable topographic position, with soil texture, topographic shelter, grazing intensity, and parent material as four covariates. Relationships

between environmental variables and stand structure (TYPE) and the number of nodes were analyzed by contingency tables and ANOVA.

RESULTS

Growth

Log-log regressions best represented the statistical relationship between height and age (Fig. 3) and diameter and age of *C. reticulata* individuals. An initial impression that regression lines do not fit the scatter of points at $\log(\text{age}) < 1.2$ can be reconciled by recognizing that the dense central elliptical clouds of points have controlled the regression results. In both cases the least-squares fit resulted in a good fit to the dense cloud of points representing middle-aged trees, but resulted in almost entirely negative residuals for trees younger than 10–25 yr. Because these younger trees were from a small number of sites, many of which showed battering by floods, distributions of residuals were judged to be acceptable.

Celtis reticulata diameter and height were tightly related in a log-log regression ($R^2 = .75$). Mean height and diameter of dominant and codominant *C. reticulata*, regardless of age, were 5 m and 18 cm, respectively. While diameter is a better predictor of age than height ($R^2 = .53$ and $.25$, respectively), height is more responsive to site characteristics than is diameter, both in the literature and in this study. Thus, height was the preferred basis for the site index.

Fifty-year-old *C. reticulata* trees in Idaho averaged 3.9 m tall and 13.6 cm in diameter. Using height, we constructed site index curves

TABLE 2. Categorization of the *Celtis reticulata* stand structure variable TYPE. TYPE represents the five types of stand structure that were recognized from the density classification. Within each stand, the three size classes of trees (juvenile, mature, decadent) were assigned to a density class based on the following definitions. Mid-point values were used as needed. **Juvenile:** (1) widely scattered—5 or fewer juveniles present; (2) scattered— >5 juveniles present in a nonaggregated distribution averaging >10 canopies apart; (3) subcontinuous—breaks in the total canopy exist but juveniles average >3 and <10 canopies apart. **Mature/Decadent:** (1) widely scattered—mature individuals >10 crown widths apart; (2) scattered—mature individuals separated by gaps of >4 and <10 individual crown widths; (3) subcontinuous—breaks in the total canopy exist but mature individuals average ≤ 3 crown widths apart; (4) continuous—mature trees form a continuous matrix with only occasional gaps.

TYPE	Description	Density class		
		Juvenile	Mature	Decadent
1	Young	≥ 1	$\leq .5$	≤ 2
2	Nonreproducing, nondecadent	$\leq .5$	$> .5$	≤ 2
3	Reproducing, nondecadent	≥ 1	≥ 1	≤ 2
4	Reproducing, decadent	≥ 1	≥ 1	> 2
5	Nonreproducing, decadent	< 1	$> .5$	> 2

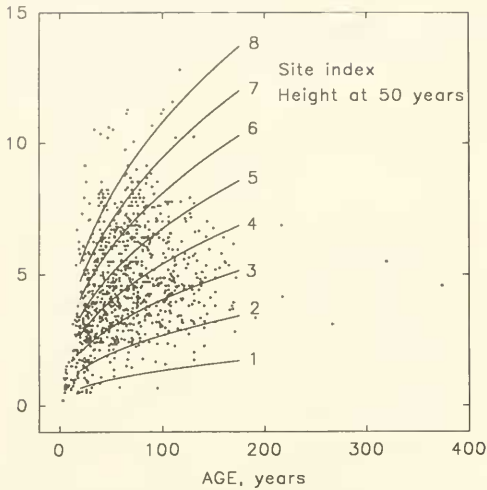


Fig. 3. Nontransformed log-log regression of *Celtis reticulata* height (m) on age and site index curves for the Idaho stands.

for Idaho *Celtis* stands to allow site classification for a stand at any age (Fig. 3). Site quality of an area can be assessed by determining average height and age of dominant trees and locating the position of these coordinates on the site index graph. The stand's site index is then read from the closest curve.

Site quality, as expressed by the height-based site index, differed among the eleven topographic positions identified ($P = .0001$, $F = 4.4$) (Table 3). However, variation within topographic positions was large, so that at the .05 significance level, only draws differed from any other specific topographic position. Growth was faster in draws than on talus slopes, upper slopes, mid-slopes, and stream terraces.

Although site index means did not differ statistically between most topographic positions, a relatively predictable biological ranking of topographic positions was expressed, with a general trend of faster growth where sheltered and mesic to slower growth on more xeric and exposed sites. For example, site index values were smallest on talus slopes, followed by upper slopes, mid-slopes, and stream terraces (Table 3).

Celtis reticulata occurred infrequently on north- and east-facing slopes (Fig. 4A). Twenty-five percent (60) of stands were found on SW slopes, with a heat load between 0.95 and 1.00, the hottest values of the heat load index; 58% (140) were between 0.74 and 1.00. Only

32 stands (13%) were located on the coolest sites between 0.00 and 0.20, or between 350° and 98° east of north. The mean heat load index was 0.69. No stands were found between 349° and 9° east of north.

In spite of *C. reticulata*'s affinity for southerly exposures, heat load was not a good predictor of hackberry growth characteristics. More often than not, stands have an affinity for southerly exposures, but because of topographic sheltering, growing conditions are often not as harsh or water stressed as they first appear. Of 241 *Celtis* stands, 168 (70%) had at least an intermediate topographic shelter.

In a stepwise regression analysis from a pool of six independent variables (soil texture, rock, grazing intensity, shelter, heat load, and slope), shelter was the most important predictor of site index ($R^2 = .13$, $P < .001$, $F = 35.5$). Site index values were largest when shelter was greatest, with well-sheltered stands differing from intermediate and open exposures (Table 4). However, variability in growth rates within a given class of shelter is large, as shown by the low R^2 .

Presence of *C. reticulata* is correlated with surface rock or rock outcrops. Of the 241 stands sampled, 96 (40%) had a surface rock cover of 50% or more (Fig. 4B). Twenty percent of the stands were extremely rocky, with rock covering 75–98% of the ground surface. Average rock cover was 39%.

A weak, inverse relationship between percent surface rock cover and site index was found ($R^2 = -.28$, $P = .0001$). As rock cover increased, site index tended to decrease slightly. Rock was a statistically significant variable in a stepwise multiple regression as well, following topographic shelter in order of entry. Including rock in the model increased the R^2 value from .13 to .20 ($F = 28.9$, $P < .001$). On sites classified as draws, where topographic shelter is maximized, surface rock cover is less important.

Neither parent material nor grazing intensity was a statistically significant predictor of site index ($P = .43$ and $.14$, respectively). However, site index values differed with soil texture ($P = .023$, $F = 2.07$). As with topographic position (Table 3), means were ranked by Fisher's LSD procedure in an intuitively predictable order. Growth rates were higher on finer-textured soils (clay or loam) than on coarse-textured soils (sand). At alpha = .05, the

TABLE 3. Site index values of *Celtis reticulata* (s = standard deviation) for each topographic position. Mean site index (SI) values have been transformed back into the original scale of measurement to aid interpretation. Topographic positions with no overlap of similarity grouping letters are different from each other at the .05 significance level (Fisher's LSD).

Topographic position	Mean SI: transformed (s)	Mean SI: back- transformed	N	Similarity grouping
Draw	0.74 (0.16)	5.5	30	A
High-water line	0.65 (0.15)	4.4	37	AB
Toe slope	0.61 (0.14)	4.1	17	AB
Rocky draw	0.58 (0.17)	3.8	15	AB
Lower slope	0.57 (0.19)	3.7	40	AB
Bench	0.56 (0.24)	3.6	16	AB
Broken lower slope	0.55 (0.12)	3.5	20	AB
Stream terrace	0.51 (0.31)	3.2	13	BC
Mid-slope	0.50 (0.18)	3.2	28	BC
Upper slope	0.48 (0.20)	3.0	12	BC
Talus slope	0.47 (0.13)	2.9	13	BC

only pairs that differed from each other were talus and loam.

Interactions between soil texture and topographic position were highly significant (Chi-square, $P = .001$). When the analysis of site index and soil texture was restricted to just upland sites, the effect was slightly more pronounced ($P = .014$, $F = 2.49$).

Growth Form

"Shrubiness" was quantified by counting the number of live and dead main stems or trunks of each individual. Regression analysis of stem number with the variables grazing intensity, topographic shelter, soil texture, heat load, slope, average height, average diameter, and percent surface rock cover produced several statistically significant, albeit weak, relationships. Live and dead stem density per individual decreased as topographic shelter increased ($R^2 = .20$ and $.30$, respectively). Average height decreased slightly as the number of live stems increased ($R^2 = .20$). In general, on sheltered sites *C. reticulata* has a single stem (treelike) rather than multi-stem (shrublike) growth form.

Differences in plant growth form were found among topographic positions and among parent materials. Individuals growing at mid-slope were generally shrubbier, with a greater number of live stems ($\bar{x} = 2.5$), than individuals growing at high-water line ($\bar{x} = 1.4$), in draws ($\bar{x} = 1.6$), and in rocky draws ($\bar{x} = 1.5$) (ANOVA, $P = .003$, $F = 2.71$). Dead stems were far less numerous than live stems and

were absent from most individuals. The number of dead stems at mid-slope ($\bar{x} = 0.6$) was greater than all other topographic positions except upper slopes ($P = .0001$, $F = 6.5$). Stands at high-water line, rocky draw, stream terrace, draw, and broken lower slope topographic positions averaged only 0.1 dead stems per individual. Growth form did not differ with the number of size modes within a stand.

Individuals on sandstone were more commonly multi-stemmed than those on the three other parent materials, for both living and dead stems ($P < .001$, $F = 8.5$; $P < .001$, $F = 14.7$, respectively).

Longevity

The mean age of individuals sampled during our study was 66 yr, with a range of 1–374 yr (Fig. 5). Old age and large size are not tightly related. For example, it is common to find trees 10 m tall but less than 75 yr old. Diameter was often a better predictor of age than was height ($R^2 = .54$ and $.26$, respectively, after log-log transformation).

The oldest *C. reticulata* recorded in this study (about 374 yr) grew on an exposed talus slope approximately 300 m above the Salmon River; it was 4.6 m tall and 48 cm in diameter at 20 cm above ground level. Percent surface rock cover of the site was 90%, with the small stand of scattered trees restricted to talus margins where pockets of soil were exposed. Other members of the stand ranged in age from 191 yr (3.35 m tall, 28 cm diam) to 320 yr (5.48 m tall, 46.5 cm diam).

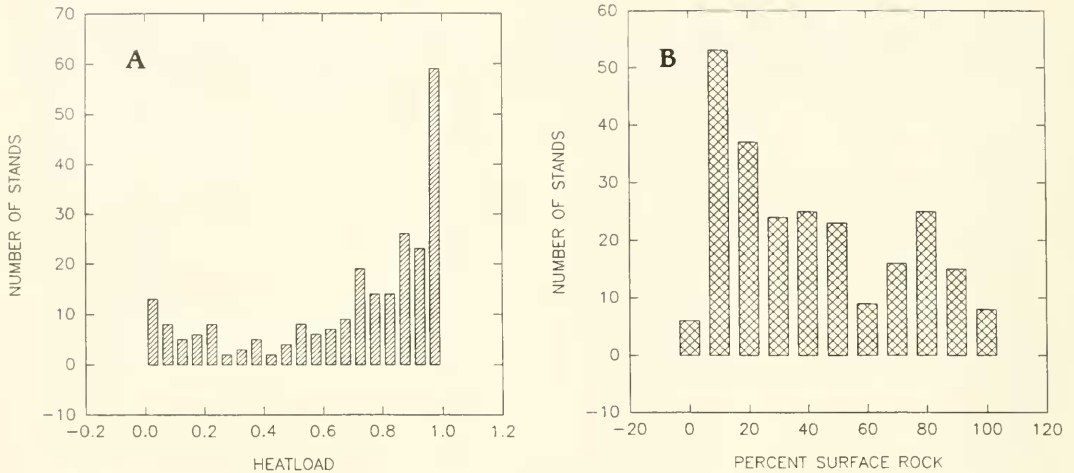


Fig. 4. Frequency distributions of the number of *Celtis reticulata* stands by (A) heat load and (B) percent surface rock cover.

Stand Structure

Of the 241 *Celtis* stands, 178 (74%) were reproducing and only 4 (1.7%) of these were decadent. Fifty-seven stands (23.5%) were classified as nonreproducing, 6 (2.5%) of them decadent. The remaining 6 stands (2.5%) were recently established (juvenile dominated), with no mature individuals present.

Structure of *C. reticulata* stands, in terms of their relative densities of juvenile and mature size classes, was unrelated to soil texture (Chi-square, $P = .31$). Structural type was weakly related to topographic position of the stand (Chi-square, $P = .08$). Of the 11 topographic positions, rocky draws had the highest juvenile density, or recruitment. In general, juvenile densities increased as the percent of surface rock cover increased. Density of *C. reticulata* juveniles was highest when rock cover was 50% or greater.

Rocky draws consistently had the densest canopies, followed by draws and high-water

line. Rocky draws were never assigned an overall density < 2.5 , where 3 = subcontinuous. In fact, 75% of rocky draws had closed or nearly closed canopies (overall density = 3.5 or 4). Juveniles were often present on the margins of rocky draws.

The few decadent stands were found higher on the slope, on steeper slopes, and in less-sheltered positions than nondecadent stands. Nonreproducing, decadent stands were more steeply sloping than young and nondecadent, nonreproducing stands (ANOVA, $P = .003$, $F = 4.03$) (Table 5). Of the 10 decadent stands, 50% were at mid-slope and 20% were on talus.

While none of the decadent stands were extremely overgrazed, their distance from water may have confounded this result. Overgrazed stands were typically found on fairly gentle terrain ($\bar{x} = 14^\circ$, S.D. = 8.6) and in close proximity to a water source, where livestock tend to concentrate, while decadent stands were on steeper slopes (Table 5) and at higher slope

TABLE 4. Mean site index (SI) values for *Celtis reticulata* for three levels of topographic shelter, in both transformed and back-transformed scales. Topographic shelters with no overlap of similarity grouping letters are different from each other at the .05 significance level (Fisher's LSD).

Topographic shelter	Mean SI: transformed (s)	Mean SI: back-transformed	N	Similarity grouping
Sheltered	0.69 (0.15)	4.9	73	A
Intermediate	0.55 (0.20)	3.6	129	B
Exposed	0.49 (0.14)	3.1	39	B

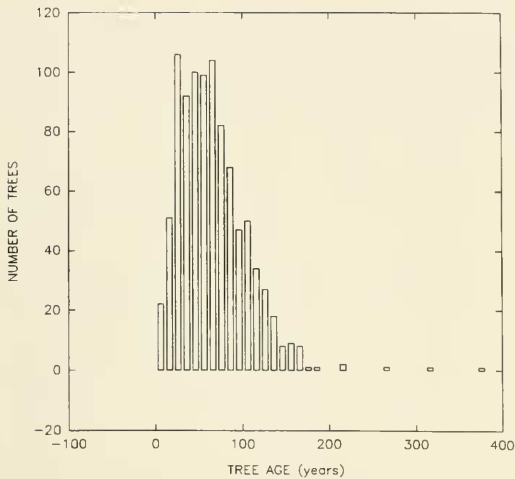


Fig. 5. Frequency distribution of the number of *Celtis reticulata* trees by tree age.

positions. Less intensively grazed stands averaged 23° (S.D. = 10.1).

Grazing level was related to stand structure (TYPE; Chi-square, $P = .0002$). A larger percentage of heavily grazed stands (53%) were nonreproducing than were stands with light or moderate grazing intensity (18.5%). Even though sample sizes were very different (light or moderate = 205, extreme = 36), the pattern confirms field observations of low recruitment under extreme grazing pressure. However, it is perhaps even more noteworthy that recruitment on heavily grazed sites is as high as it is, given how few, if any, other shrub species are present on such sites.

Among the four parent materials, 37% of *C. reticulata* stands growing on sandstone were nonreproducing, as compared to 21%, 22%, and 21% of stands growing on granite, basalt, and river alluvium, respectively (Chi-square, $P = .014$; Table 6). A greater number of sandstone-associated stands were nonreproducing than expected (14 and 9, respectively), while fewer were reproducing than expected (22 and 27, respectively). Expected and observed values for the three other parent materials were more similar.

Newly established *C. reticulata* stands are apparently rare, as few were observed during the study in spite of efforts to locate them. Only six young (<33 yr) stands were sampled. These were typically on rocky sites with intermediate topographic shelter and gentle slopes

TABLE 5. Average slopes of decadent, nondecadent, and young stands of *Celtis reticulata*, with the variable TYPE in its original five-category format. TYPE represents the five types of *Celtis reticulata* stand structure that were recognized.

TYPE	N	Mean slope (degrees)	S.D.
Young (juvenile)	6	12	3.4
Nonreproducing, nondecadent	51	20	9.6
Reproducing, nondecadent	174	22	10.3
Reproducing, decadent	4	27	7.7
Nonreproducing, decadent	6	33	5.0

($\bar{x} = 12^\circ$). All had at least 15% surface rock cover, but most had 75% or greater rock cover ($\bar{x} = 65\%$). Five of the six stands were on alluvium, including stream terraces, high-water lines, and benches. All five had sandy soil. The sixth stand was atypical, occurring near a mid-slope, sparsely vegetated band of sandstone with intermediate shelter. All individuals were shrubby, decadent, and old (18–33 yr) relative to the average height of 0.7 m (expected age = 8 yr). Soils were sandy loam in texture.

While young stands were only on sites with intermediate topographic shelter, reproducing and nonreproducing stands differed little in the degree of shelter they received (Chi-square, $P = .06$). Thirty-three percent of reproducing stands were sheltered, compared to 25% of nonreproducing stands.

The amount of surface rock differed weakly across stand structure (TYPE; ANOVA, $P = .038$, $F = 2.58$). Differences were greater when the variable TYPE was restructured to three categories (mature reproducing, mature nonreproducing, young), eliminating decadence as a factor (ANOVA, $P = .015$, $F = 4.26$). Under the three-level categorization, young stands were rockier than mature, nonreproducing stands ($\bar{x} = 32\%$) but did not differ from those that were reproducing.

Number of Modes

Celtis reticulata stands typically appeared to be unimodal (73%), with one dominant cohort. Stands with two modes were far less common (11%), but a slightly greater number were all-aged (16%). Since only two stands had three modes, they were dropped from analyses;

TABLE 6. Cross tabulation of the number of *Celtis reticulata* stands by stand structure and parent material. The hypothesis of independence of stand structure and parent material is rejected with $P = .014$.

Parent material	Observed/ expected	Mature			Row total	Row %
		Nonreprod.	Reprod.	Young		
Granite	obs.	11.0	40.0	0.0	51	21
	exp.	12.2	37.6	1.3		
Sandstone	obs.	14.0	22.0	1.0	37	16
	exp.	8.8	27.2	0.9		
Basalt	obs.	20.0	71.0	0.0	91	38
	exp.	21.5	66.3	2.3		
Alluvium	obs.	12.0	45.0	5.0	62	25
	exp.	14.5	44.9	1.5		
Column total	obs.	57.0	178.0	6.0	241	100
Column %		24%	74%	3%		

thus, the sample size for this portion of the results is based on 239 stands. Growth form or number of stems of the individuals was unrelated to number of modes.

Although of marginal statistical significance, all-aged stands were more common on sheltered sites (Chi-square, $P = .07$). For example, 33% of stands in draws, which typically have at least an intermediate topographic shelter, were all-aged. The percent of all-aged stands at other topographic positions ranged from 6% to 16%.

Livestock grazing intensity may restrict entry of new cohorts within a *C. reticulata* stand as shown by the strong tendency for overgrazed stands to be unimodal (92%; Chi-square, $P = .0008$). In contrast, 70% of light to moderately grazed stands had only one mode, 11% were bimodal, and 18% were all-aged.

Size structure of *Celtis* stands did not differ with topographic position, parent material, soil texture, slope, percent surface rock, or heat load (all $P > .2$).

DISCUSSION

In our study, trees were typically tallest and least shrubby when located in draws, on sites with surface or subsurface moisture, and in areas where they received maximum topographic shelter. Similar observations of *C. reticulata* have been recorded by others (Eliot 1938, Van Dersal 1938, Peattie 1953), and for different species of *Celtis* as well. For example, Hitchcock and Cronquist (1964) noted that *Celtis reticulata* is taller in moist areas in the Pacific Northwest. In Oklahoma, *C. laevigata* (sugarberry) is typically a small tree in open areas, but in lowland forests it reaches its maximum

development (Schnell et al. 1977). On the eastern Great Plains, *C. tenuifolia* (dwarf hackberry) is a gnarled, shrublike tree when growing on its typical rocky, shallow, calcareous substrate, but in the bottom of ravines it may reach heights of 8–10 m (Stephens 1973). In addition to the influence of an ameliorated environment, sheltered stands may be less prone to repeated disturbances such as fire, to which a vegetative sprouter such as *C. reticulata* will often respond with a shrubbier growth form.

In Oklahoma, *Celtis* occurs almost exclusively on loamy bottomland soils (Dooley and Collins 1984), and in west Texas it is best developed on alluvium (Van Auken et al. 1979). In the canyon grasslands of Idaho, Tisdale (1986) recognized two types of *Celtis*-dominated vegetation on soils of two principal origins. The *C. reticulata*-*Agropyron spicatum* habitat type occurs on lower valley slopes with rocky (50–60%), weakly developed loam soils derived from residual and colluvial materials. The second vegetation type, unclassified because of heavy livestock disturbance and alien plant dominance of the understory, occurs on alluvial terraces with deep sandy soils.

Soil texture appears to have a greater influence on *C. reticulata* growth on upland sites than on sites associated with a perennial water source. While *C. reticulata* grows on a range of soil textures in Idaho, we found the tallest trees on loams, possibly because of their greater water-holding capacity and nutrient content. However, 80% of the stands occurred on soils with some sand component, and 30% were on sand or coarse sand. The presence of good drainage may be an important limiting

factor for *C. reticulata*, as finer-textured soils of the uplands were nearly always skeletal. The increased percolation of sandy or skeletal soils provides greater moisture availability for deep-rooted shrub and tree species.

In Idaho, *C. reticulata* is most prevalent on rocky sites with southeast to westerly aspects, although heat load was not an important predictor of growth. The presence of rock, particularly bedrock, may in fact be critical for hackberry's existence on certain sites. It may also partially explain the fragmented distribution of the species in Idaho. Other rock-associated species have been observed in semiarid regions as well. In the shrub-steppe region of eastern Montana, Rumble (1987) found that scoria rock outcrops provide a unique habitat for several relatively mesic species. *Rhus trilobata* (skunkbush sumac), *Prunus virginiana* (chokecherry), *Ribes* spp. (currant), and *Juniperus* spp. (juniper) were found only in association with rock outcrops in that ecosystem. He concluded that their occurrence is probably related to protection from wind, snowdrift accumulation, shading, and mulch effects of rocks. Oppenheimer (1964) and Potter and Green (1964) suggested that the association of mesic species with rocky substrates is due to temporary water reservoirs that rock fissures provide. In Arizona, Johnsen (1962) reported that *Juniperus monosperma* (one-seed juniper) is largely limited to rock outcrops, where he recorded 2–2.5 times as much available moisture. The theory of extra moisture availability in rock fissures could also hold true for the deeply rooted *C. reticulata*, helping explain its frequent presence on southerly aspects.

Other plausible explanations for the infrequency of *C. reticulata* on northerly aspects and sites with less surface rock cover include its sensitivity to late spring frosts (personal observation) and poor competitive ability with fast-growing species. In Idaho, *C. reticulata* is the last shrub to break dormancy and expand its leaves in the spring. This strategy, in combination with the tendency to grow on warmer slopes, generally prevents frost damage from occurring. The greater effective soil moisture and dense vegetative cover of north slopes probably create an environment too competitive for this slow-growing species.

In summary, *Celtis reticulata* can generally be described as slow-growing and small-statured. Fifty-year-old trees averaged 4 m tall

and 13.6 cm in diameter in Idaho, with a mean tree height and diameter, regardless of age, of 5 m and 18 cm, respectively. Unlike some shrub and tree species in the Intermountain West, populations are generally maintaining themselves by vegetative sprouting or seedling recruitment, despite historic and prevailing large-scale habitat alterations resulting from overgrazing, exotic plant invasion, and changing fire frequencies (Tisdale 1986, Whisenant 1990). Hackberry's general resiliency and ability to resprout following disturbance or injury likely play a role in this, as does its positive association with rock. Recruitment, as expressed by the density of juvenile individuals, increased as surface rock cover increased. However, under extreme grazing pressure, recruitment was significantly lowered and stands were nearly all unimodal. All-aged stands were absent from severely grazed sites. Even though rock favors *Celtis* recruitment, its growth is favored on less-rocky sites, such as draws.

The most likely explanation for relatively slow *C. reticulata* growth on stream terraces, in spite of the assumed availability of groundwater, is the extreme annual fluctuation of the water level and battering by flood debris. These sites are located below the high-water line. Above the high-water line the mean site index is larger and mechanical stresses are less extreme. While newly established *C. reticulata* stands were uncommon, they typically occurred on these riparian sites, where establishment conditions occur more frequently than in the uplands.

Although individuals are often slow-growing, the variation in site conditions that the species appears to tolerate and its other positive attributes (i.e., wildlife food, cover, landscape structure, potential large size, tolerance of southerly aspects), are favorable qualities for those seeking rehabilitation species. The species' persistence in heavily degraded ecosystems may speak to its suitability for rehabilitation projects as well.

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